

EVOLUTION OF THE SANTA LUCIA FIR (*ABIES BRACTEATA*) ECOSYSTEM¹

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ABSTRACT

Abies scherrii Axelrod is described from the Miocene of western Nevada, and it resembles the living *A. bracteata* of the Santa Lucia Mountains, coast-central California, a unique endemic representing the sole member of the subgenus *Pseudotorreya*. Although the fossil species *A. chaneysi* Mason and *A. longirostris* Knowlton have previously been considered allied to *A. bracteata*, those species are extinct, they are not closely allied to *bracteata*, and they are only distantly related to living Asian firs. *A. scherrii* occupied an ecotone between broadleaved evergreen sclerophyll forest and mixed conifer forest during the Miocene in western Nevada, and its descendant *A. bracteata* has a similar occurrence today. The Miocene communities were much richer than the living, including species whose nearest descendants occur only in regions with summer rainfall, or now occupy more restricted areas in California. The latter include *Sequoiadendron* of the central and southern Sierra Nevada, species of *Chamaecyparis* and *Picea* that are confined to the Klamath-Siskiyou region of northwestern California, and species of *Abies* and *Pinus* that are largely subalpine in the Sierra Nevada. *Abies scherrii* and its associates shifted coastward as colder and drier climate developed over the interior. *Abies bracteata* has survived in a near-coastal climate where evaporation rate is not so high as in the interior or in areas to the south, and where it is largely removed from regular heavy winter snow and ice. Some of its associates were segregated into their present areas as the summer-dry mediterranean climate emerged in the Quaternary. *Sequoiadendron* was confined to the relatively drier and sunnier central and southern Sierra Nevada where there was sufficient light in an open forest to enable it to reproduce. *Chamaecyparis* and *Picea* were restricted to the northwest sector where there is a longer precipitation season, some summer rain, and where evaporation rate is lower than in the Sierra. Present subalpine species of *Abies*, *Pinus* and *Tsuga* were eliminated from the mixed conifer forest in the Sierra Nevada as evaporation rate increased during summer and produced conditions inimical for seedling establishment, though they still persist in the upper mixed conifer forest in moister, more equable areas to the northwest. *A. bracteata* may have had a wider distribution in the Coast Ranges during the moister phases of the Quaternary, together with the mixed conifer forest species. It was apparently restricted with them as drier, hotter climates spread during the later postglacial periods.

Santa Lucia fir (*Abies bracteata*) is confined to the middle and upper slopes of the Santa Lucia Mountains, coast-central California (Figs. 1–2). Among the 60-odd species and varieties of fir it is the sole member of the subgenus *Pseudotorreya*, the remainder representing the subgenus *Abies* (Liu, 1971). Its uniqueness is seen in the long-fusiform to ovoid-conical resinless winter buds, the cones with exserted awllike bracts 2 to 4 cm long, the sharply-pointed deep green needles like those of *Torreya*, the very thin bark (and hence the need for fire protection), and its tall spirelike habit that recalls that of *Abies lasiocarpa* or *Picea engelmannii* near timberline.

The problem of its geologic history was raised by the recent discovery of a slab of shale on which are preserved three cone scales with long, exserted awllike bracts of a fir that indubitably represent a species similar to the living *A. bracteata*. This fossil, from the Late Miocene (13 m.y.) Purple Mountain flora of western Nevada, supplements a needle collected earlier at a nearby site that is similar to

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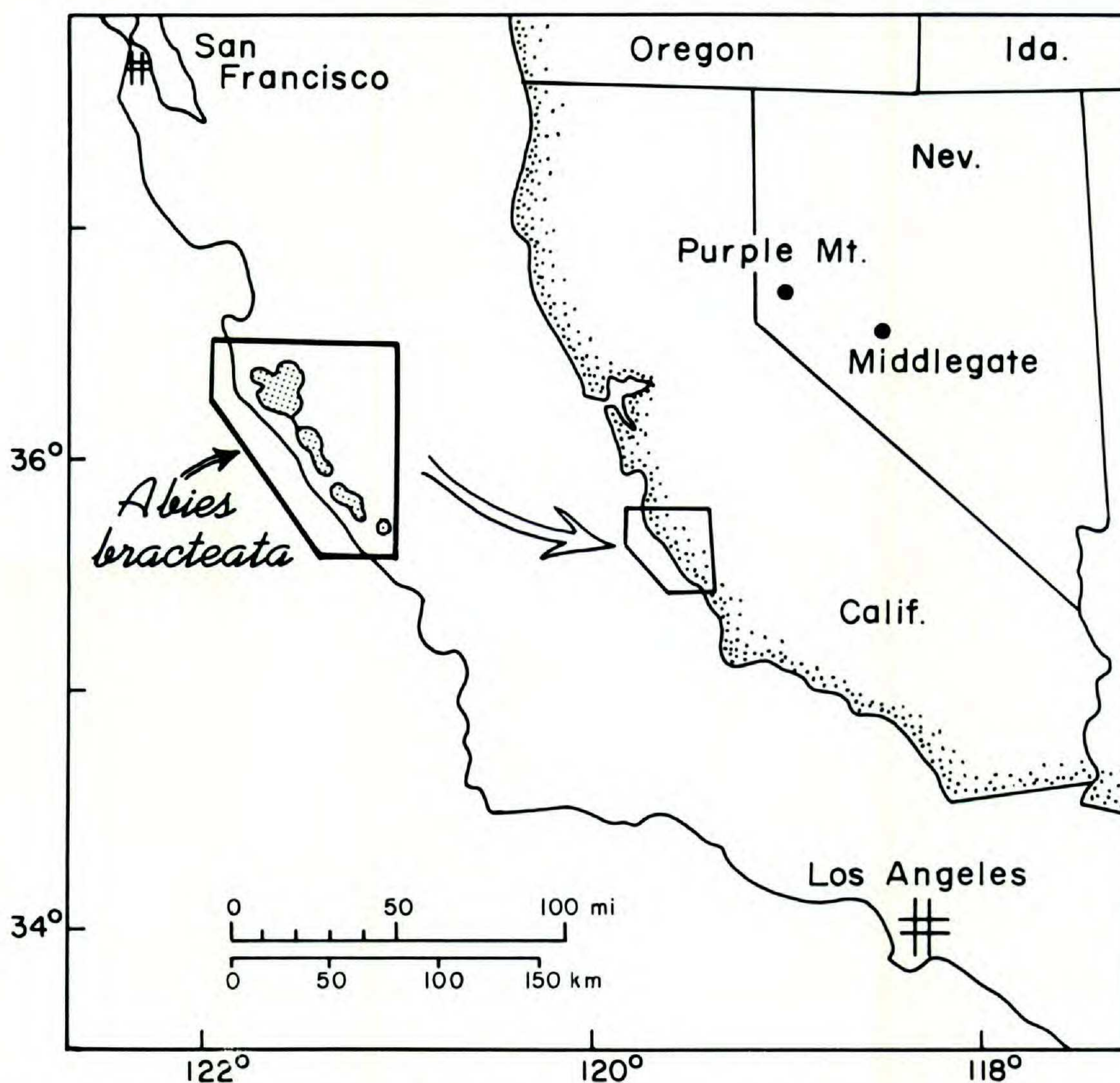


FIGURE 1. Present occurrence of *Abies bracteata* (see Griffin & Critchfield, 1972), and of the closely similar *A. scherrii* in the Miocene of Nevada.

those produced by *A. bracteata*. In addition, new collections of the slightly older Middlegate flora (Axelrod, 1956), situated about 80 miles southeast, have yielded a needle and winged seed that also represent fossil Santa Lucia fir.

In each area the associated flora is composed of broadleaved sclerophylls (*Arbutus*, *Castanopsis*, *Lithocarpus*, *Quercus*) similar to species that live with Santa Lucia fir today. Both floras also have species of *Abies*, *Picea*, *Pinus*, *Pseudotsuga*, *Chamaecyparis*, *Sequoiadendron* (Figs. 4–20) and numerous dicots that now contribute to mixed conifer forest in the Sierra Nevada, Siskiyou-Klamath Mountains, and the high Coast Ranges. The Purple Mountain and Middlegate records thus provide a basis for comparing the Miocene ecosystem at two different sites of slightly different age, and for outlining the post-Miocene history of the community.

GEOLOGIC OCCURRENCE

PURPLE MOUNTAIN FLORA

The site that yielded the Purple Mountain fossils allied to the living Santa Lucia fir is in the Truckee River canyon southwest of Wadsworth, Nevada (Figs. 1, 3). Regional geologic reports (Rose, 1969; Bonham, 1969), coupled with my



FIGURE 2. Santa Lucia fir on east slope of Cone Peak, altitude \sim 4,300 feet. *Pinus lambertiana* on left. *Quercus chrysolepis* in foreground is part of the evergreen sclerophyll forest that covers the nearby and distant slopes and includes *Arbutus menziesii*, *Lithocarpus densiflorus*, and *Quercus wislizenii* as codominants, all represented by fossils associated with *Abies scherrii* in the Nevada Miocene.

own more detailed mapping in this local area, show that the plant-bearing beds are in the lower part of the Chloropagus Formation. It is composed chiefly of andesite flows but includes mudflow breccias and interbedded thin sections of limestone and organic shale that contain the remains of plants that lived on the borders of shallow ponds and small lakes. The Chloropagus is overlain by welded dacitic tuffs of the Kate Peak Formation, dated in the nearby region at 12–13 m.y. (Bonham, 1969). The Chloropagus rests unconformably on a 50-foot rhyolite tuff that has been correlated with the Old Gregory Formation in the hills west of Fallon. It lies unconformably on black flows of Alta Andesite, which in turn rests on the varicolored welded tuffs of the Hartford Hill Rhyolite (22 m.y.). The Hartford Hill covers a peneplaned basement of high grade metamorphic rocks intruded by granodiorite of Cretaceous age.



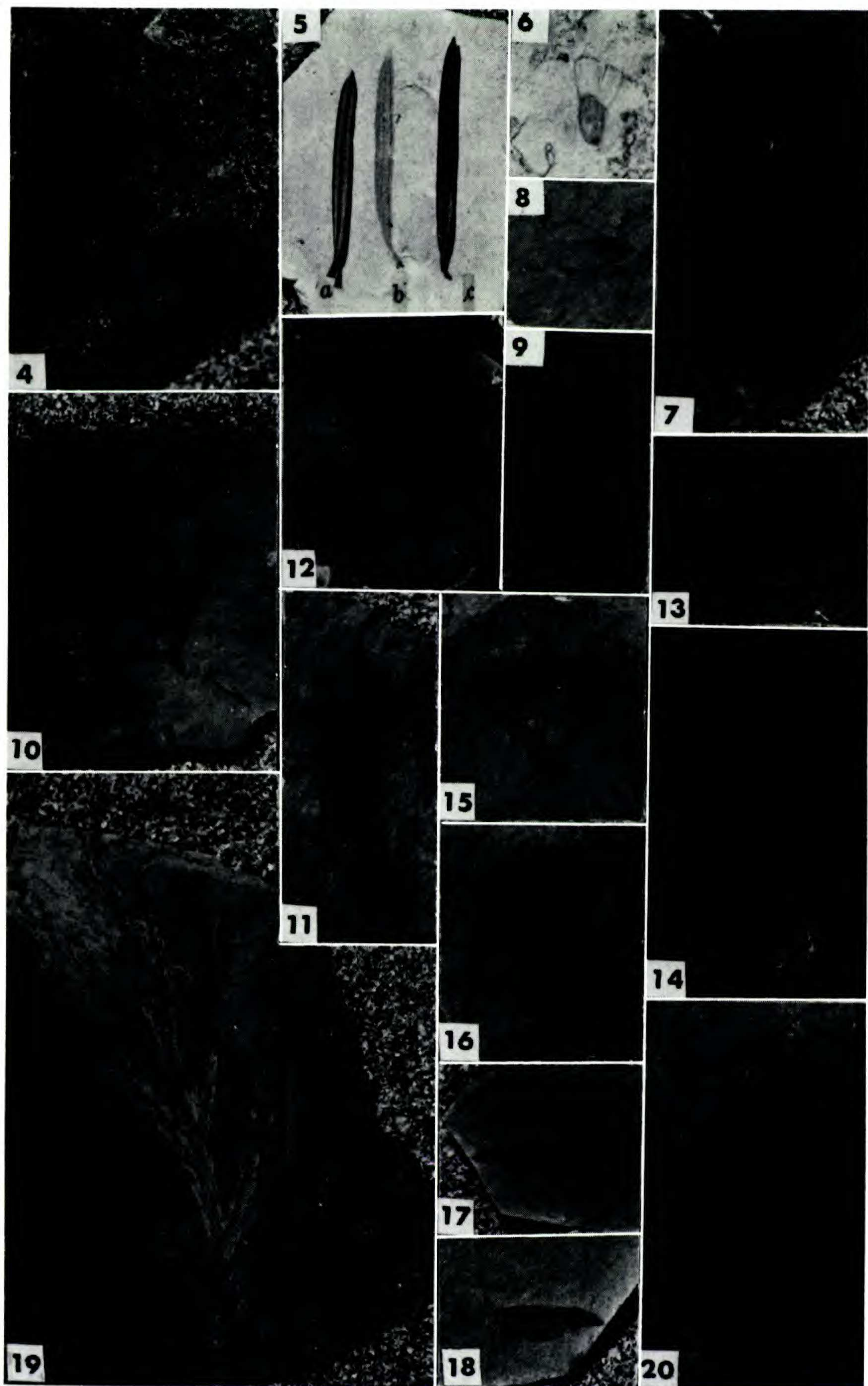
FIGURE 3. The Late Miocene Purple Mountain flora occurs in thin lake beds intercalated with andesites of the Chloropagus Formation on the low spur at the right, in the bank of the drainageway, and at the position of the observer. View is north, across Truckee River floodplain.

Flows in the basal part of the Chloropagus Formation in Fort Defiance Canyon 10 miles north of the fossil locality have been dated as 14 m.y., and a vitric tuff in the upper part of the sequence in Pierson Canyon 5 miles northwest is 13 m.y. The flora is therefore about 13.5 m.y. and is correlative approximately with the Late Miocene Fallon, Chloropagus, and Aldrich Station floras in the nearby region (Axelrod, 1956).

MIDDLEGATE FLORA

This flora comes from a site on the north side of Middlegate basin, 5 miles northwest of Eastgate, Nevada (Axelrod, 1956). The plants are preserved in white to light gray, well-bedded opaline shales interbedded with fine vitric tuff now altered to bentonite. The shales are 50–80 feet below the top of the Middlegate Formation. They grade down into soft dark mudstone, very thin opaline shale, and with local conglomerates situated opposite the mouths of small streams that entered the lake. The Middlegate Formation rests on diverse welded tuffs and flows of the Clan Alpine Volcanics directly north of the site. Since the flora was derived from volcanic slopes facing south, the warm dry exposure accounts for the rich representation of sclerophylls there.

The Middlegate is overlain conformably by fine sandstone, mudstone, tuff, and conglomerate of the Monarch Mill Formation, the basal part of which has now yielded a rich (30+ taxa) mammal fauna of transitional Hemingfordian–Barstovian (~ 16 m.y.) age.



FIGURES 4-20. Purple Mountain conifers associated with *Abies scherrii*.—4. *Abies scherrii* Axelrod, no. 5489.—5b. *Abies scherrii* Axelrod, no. 5491 from Middlegate; 5a, 5c. *Abies bracteata* needles for comparison.—6. *Abies scherrii* Axelrod, no. 5492 from Middlegate.—7-9. *Pseudotsuga sonomensis* Dorf, nos. 5493-5495.—10-11. *Chamaecyparis sierrae* Condit, nos. 5496-5497.—12. *Abies concoloroides* Brown, no. 5498.—13-14. *Pinus quinifolia* Smith, nos. 5501-5502.—15-16. *Abies klamathensis* Axelrod, nos. 5499, 5500.—17-18. *Picea sonomensis* Axelrod, nos. 5503, 5504.—19-20. *Sequoiadendron chaneyi* Axelrod, nos. 5505, 5506.

SYSTEMATIC CONSIDERATIONS

The Nevada occurrences of a Miocene fir similar to the living *A. bracteata* is not the first report of a fossil that has been presumed related to it. *Abies chaneyi* Mason from Oregon (Mason, 1927; Chaney & Axelrod, 1959) and *A. longirostris* Knowlton from Colorado (Knowlton, 1923; MacGinitie, 1953) have also been considered allied to *A. bracteata*. However, comparisons now indicate they are not closely related to it, and some of these fossils certainly represent genera other than *Abies*. Thus, it is necessary first to clarify the status of the fossil records that have been presumed allied to *A. bracteata*, following which the history of Santa Lucia fir, and the community of which it forms a part, can be outlined in provisional manner.

***Abies scherrii* Axelrod sp. nov.**—FIGS. 4, 5b, 6.

Cone scales 9–12 mm broad, 6–8 mm long, broadly oblong to ovate, distal end truncate to broadly rounded, proximal part truncated, with thin, straight woody peg of attachment; bract exserted, over 2.3 cm long, awllike, 1 mm wide for most of length but widening to 2 mm in proximal 3 to 4 mm; lateral appendages not visible on exposed upper surface. Needles 2.0–2.8 cm long, broadest at middle, 2.5 mm; apex sharply acuminate, petiole somewhat curved, sharply truncated. Winged seed 12 mm long, wing terminal, 5 mm long, somewhat torn, about 5 mm wide distally; seed long-oval, 7 mm long, 3 mm broad.

This species is represented in the Purple Mountain flora by a slab containing 3 cone scales with bracts and by a second specimen on which is a poorly preserved needle. In the Middlegate flora a winged seed and a needle are referred to this species.

The cone scales and attached bracts are similar to those of the living *A. bracteata* of the Santa Lucia Mountains, coast-central California. The lateral lobes of the bract are not visible, but this appears to be the result of curling so that they cannot be seen on the lower (inner) preserved surface. The needles and the single winged seed are also similar to those produced by the living Santa Lucia fir.

This species is named for Annette K. Scherr, a student in my course in Forest History who, during a class field-trip to the Purple Mountain area, collected the slab of shale on which are preserved the diagnostic cone scales of fossil Santa Lucia fir, *Abies scherrii*.

Occurrence: Nevada, Purple Mt.: U.C. Mus. Pal. holotype no. 5489, hypotype no. 5490. Nevada, Middlegate: U.C. Mus. Pal. hypotype nos. 5491, 5492.

***Abies chaneyi* Mason**, Publ. Carnegie Inst. Wash. 347: 149, *pl. 4, figs. 1 and 7* (winged seeds only), *fig. 2*. 1927. Chaney & Axelrod, Publ. Carnegie Inst. Wash. 617: 137, *pl. 11, fig. 3*. 1959. Axelrod, Univ. Calif. Publ. Geol. Sci. 51: 141 (winged seeds only). 1964.

These cited specimens are winged seeds except for one that represents a cone scale with attached bract (Mason, *pl. 4, fig. 2* only). The seeds have a slender, generally oblong to long-oval outline and the long narrow wing is attached high

up on the seed and is not appreciably widened or asymmetrical distally. The cone scale has a long exserted bract that is much wider at the distal edge of the scale than those of the living *A. bracteata*.

These fossils are not closely related to any living fir. Although the winged seeds resemble those produced by the living *A. bracteata*, those of other species—notably *A. chensiensis* Van Tiegham of central and southern China and *A. delavayi* Franchetti of southern China—are also similar to them. The winged seeds of *A. chaneyi* resemble those of *A. longirostris* Knowlton from the Creede flora of Colorado (Knowlton, 1923), though the Creede specimens tend to average somewhat smaller in size. However, the Creede fir has cone scales with exserted bracts that are inseparable from the Mascall fossil (Mason, 1927: 4, fig. 2). In this regard, the Creede *A. longirostris* appears distantly related to *A. delavayi* of southern China, as judged from the winged seeds as well as the conspicuously exserted acuminate bract. Further affinity is also seen in the fact that typical fir foliage is well represented in the Creede flora. It is like that produced by many montane species, with the needles curved upward on the branchlets, a feature also exhibited by *A. delavayi*.

Present evidence indicates that *A. chaneyi* is more nearly related to *A. longirostris* Knowlton than to any other fossil or living fir, and it may have been derived from the Creede species. Although both species seem distantly related to *A. delavayi* of southern China, there is no evidence of any close affinity between them and the living *A. bracteata* of the Santa Lucia Mountains.

Occurrence: Oregon, Mascall: U.C. Mus. Pal., holotype no. 135, hypotype no. 5488, A, B (on same slabs as foliage specimens of *Cephalotaxus*, = "*Abies chaneyi*" branchlet, nos. 134, and 136), 2826, 2828 (its counterpart), homeotype no. 2827. Oregon, Beulah: U.C. Mus. Pal. homeotypes nos. 779–780 (winged seeds only).

Cephalotaxus bonseri (Knowlton) Chaney & Axelrod, Publ. Carnegie Inst. Wash. 617: 136, *pl. 11, fig. 13*. 1959 (see synonymy).

Abies chaneyi Mason, Publ. Carnegie Inst. Wash. 346: 149, *pl. 4, figs. 1, 6* (counterparts of twig; not winged seed which remains *A. chaneyi* Mason). Chaney & Axelrod, Publ. Carnegie Inst. Wash. 617: 137, *pl. 11, figs. 1–2* only (fig. 3 remains *A. chaneyi* Mason). 1959. Axelrod, Univ. Calif. Publ. Geol. Sci. 51: 141. 1964 (in part).

Torreya bonseri (Knowlton) LaMotte, Publ. Carnegie Inst. Wash. 455: 108, *pl. 3, fig. 9*. 1936.

The above-cited specimens of *Abies chaneyi* are similar to the leafy twigs and needles of *Cephalotaxus bonseri*, a species abundantly represented in the Mollala flora of western Oregon, and known also from the Spokane (Latah) and Neroly floras of Washington and California, respectively (Chaney & Axelrod, 1959: 136). The needles are not *Abies* because they do not have the typical rounded bases, nor are the petioles twisted prominently as in *A. bracteata*. Furthermore, the leafy twigs do not reveal the rounded leaf scars that are diagnostic of *Abies*. However, the longitudinal ridging on the fossil twigs is like that on the twigs of the living *Cephalotaxus fortunei* of central China, which bear long, sharply acuminate needles like the fossils, and they often are curved in a falcate manner much like the fossil foliage.

Occurrence: Mascall, Ore. hypotype nos. 134 and 136 (counter parts), homeotype no. 2829 (leafy branch); Stinking Water, Ore.: hypotypes nos. 2830, 2831, homeotypes nos. 2832,

2833; Beulah, Ore.: homeotypes nos. 8573–8579 (needles only); 49-Camp, Nev.: hypotype no. 777.

Summarizing, *Abies scherrii* from the Middle and Late Miocene of western Nevada is similar to the living *A. bracteata*. Reexamination of the fossil *A. chaneyi* Mason and *A. longirostris* Knowlton, previously considered related to *A. bracteata*, shows that they are not allied to it. They seem related to one another, and may be extinct members of an alliance of present Asian distribution, of which *A. delavayi* of southern China is a surviving relict.

COMPOSITION

As now known, *Abies scherrii* occurs in the Purple Mountain and Middlegate floras of western Nevada. Among its associates that are common to both floras are the species listed in Table 1. As might be expected, each flora has species that are not now known from the other site. Species in the Purple Mountain flora that are not recorded at Middlegate are listed in Table 2.

TABLE 1. Species associated with *Abies scherrii* in both the Purple Mountain and Middlegate floras.

Fossil Species	Similar Living Species	Fossil Species	Similar Living Species
<i>Abies concoloroides</i>	<i>A. concolor</i>	<i>Lithocarpus klamathensis</i>	<i>L. densiflorus</i>
<i>Abies klamathensis</i>	<i>A. shastensis</i>	<i>Quercus hannibalii</i>	<i>Q. chrysolepis</i>
<i>Picea sonomensis</i>	<i>P. breweriana</i>	<i>Mahonia simplex</i>	<i>M. japonica</i> ; <i>M. lomariifolia</i>
<i>Picea magna</i>	<i>P. polita</i>	<i>Mahonia reticulata</i>	<i>M. pinnata-insularis</i>
<i>Pinus quinifolia</i>	<i>P. monticola</i>	<i>Amelanchier alvordensis</i>	<i>A. alnifolia</i>
<i>Pseudotsuga sonomensis</i>	<i>P. menziesii</i>	<i>Cercocarpus antiquus</i>	<i>C. betuloides</i>
<i>Chamaecyparis sierrae</i>	<i>C. lawsoniana</i>	<i>Cercocarpus holmesii</i>	<i>C. paucidentatus</i>
<i>Sequoiadendron chaneyi</i>	<i>S. giganteum</i>	<i>Heteromeles sonomensis</i>	<i>H. arbutifolia</i>
<i>Populus eotremuloides</i>	<i>P. trichocarpa</i>	<i>Lyonothamnus parvifolia</i>	<i>L. extinct</i>
<i>Populus payettensis</i>	<i>P. angustifolia</i>	<i>Sorbus</i> sp. nov.	<i>S. aucuparia</i>
<i>Populus pliotremuloides</i>	<i>P. tremuloides</i>	<i>Acer columbianum</i>	<i>A. glabrum</i>
<i>Salix knowltonii</i>	<i>S. lemmonii</i>	<i>Acer middlegateii</i>	<i>A. saccharinum</i>
<i>Salix</i> sp. nov.	<i>S. melanopsis</i>	<i>Acer oregonianum</i>	<i>A. macrophyllum</i>
<i>Salix wildcatensis</i>	<i>S. lasiolepis</i>		
<i>Betula lacustris</i>	<i>B. papyrifera</i>		

The taxa that have been found in the Middlegate but are not now known from the Purple Mountain flora are listed in Table 3.

TABLE 2. Species associated with *Abies scherrii* in only the Purple Mountain flora.

Fossil Species	Similar Living Species	Fossil Species	Similar Living Species
<i>Salix</i> sp. nov.	<i>S. nigra</i>	<i>Ceanothus leitchii</i>	<i>C. velutinus</i>
<i>Castanopsis sonomensis</i>	<i>C. chrysophylla</i>	<i>Rhamnus precalifornica</i>	<i>R. californica</i>
<i>Holodiscus idahoensis</i>	<i>H. glabrescens</i>	<i>Arbutus matthesii</i>	<i>A. menziesii</i>
<i>Amorpha oklahomensis</i>	<i>A. fruticosa</i>	<i>Leucothoe</i> sp. nov.	<i>L. davisiae</i>

TABLE 3. Species associated with *Abies scherrii* in only the Middlegate flora.

Fossil Species	Similar Living Species	Fossil Species	Similar Living Species
<i>Pinus florissantii</i>	<i>P. ponderosa</i>	<i>Crataegus middlegateii</i>	<i>C. chrysophylla</i>
<i>Salix owyheeana</i>	<i>S. hookeriana</i>	<i>Prunus morganensis</i>	<i>P. emarginata</i>
<i>Salix hesperia</i>	<i>S. lasiandra</i>	<i>Acer minor</i>	<i>A. negundo</i>
<i>Alnus harneyana</i>	<i>A. tenuifolia</i>	<i>Rhus alvordensis</i>	<i>R. glabra</i>
<i>Betula vera</i>	<i>B. lenta</i>	<i>Ceanothus precuneatus</i>	<i>C. cuneatus</i>
<i>Quercus wislizenoides</i>	<i>Q. wislizenii</i>	<i>Styrax middlegateii</i>	<i>S. californica</i>
<i>Mahonia</i> sp. nov.	<i>M. nervosa</i>	<i>Diospyros andersonae</i>	<i>D. virginiana</i>
<i>Hydrangea bendireii</i>	<i>H. aspera</i>	<i>Arbutus prexalapensis</i>	<i>A. arizonica</i>
<i>Platanus paucidentata</i>	<i>P. racemosa</i>	<i>Fraxinus millsiana</i>	<i>F. anomala</i>
<i>Platanus dissecta</i>	<i>P. extinct</i>	<i>Fraxinus coulteri</i>	<i>F. oregona</i>

The differences in composition are attributable to two factors. First, the Middlegate sample is larger (7,200 specimens) than that at Purple Mountain (1,200 specimens), so it would be expected to have more numerous species (50 vs. 35 taxa). Second, the somewhat greater age of the Middlegate (15–16 m.y.) as compared with Purple Mountain flora (13 m.y.) accounts for the more numerous exotic taxa (*Acer tyrrellii*, *Betula vera*, *Crataegus middlegatei*, *Diospyros andersonae*, *Hydrangea bendirei*, *Platanus dissecta*) in it. Nonetheless, it is noteworthy that the lists include many species which, in terms of their closest modern relatives, are associated frequently at the present time. Hence, the floristic differences are not as great as one might otherwise suppose. This becomes apparent if we compare the principal vegetation types that the modern species similar to the fossils represent, as well as other aspects of the paleoecology of these floras.

PALEOECOLOGY

VEGETATION

Broadleaved Evergreen Forest.—Fossil Santa Lucia fir (*Abies scherrii*) occurs in floras in which broadleaved sclerophylls are commonly dominant. *Quercus hannibalii*, which is similar to the living *Q. chrysolepis*, makes up 85% of all specimens in the Middlegate flora, and it also dominates several of the 10 florules in the Purple Mountain area. *Abies bracteata*, which is similar to the fossil *A. scherrii*, is regularly associated with a dominant *Quercus chrysolepis* sclerophyll community in areas of its optimum development. Among its more common associates that make up broadleaved evergreen forest that interfingers with patches of conifer forest in the higher Santa Lucia Mountains are *Arbutus menziesii*, *Lithocarpus densiflorus*, and *Quercus wislizenii*, all with close equivalents in the western Nevada floras. Many of their associates have analogues in the Miocene floras that have fossil Santa Lucia fir, notably *Acer negundo*,³ *Acer macrophyllum*,³ *Ceanothus cuneatus*, *Cercocarpus betuloides*, *Heteromeles arbutifolia*, *Platanus racemosa*,³ *Rhamnus californica*, *Salix lasiandra*,³ and *Salix melanopsis*.³

³ Chiefly riparian.

Other taxa in these floras have their nearest relatives in sclerophyll vegetation in areas of summer rainfall, from southern Utah and Arizona to western Texas and southward into Mexico, notably *Acer grandidentatum*, *Arbutus arizonica*, *Cercocarpus paucidentatus*, *Fraxinus anomala*, *Fraxinus velutina*,³ *Populus angustifolia*³ (rare in So. Calif.), and *Robinia neomexicana*.

Mixed Conifer Forest.—The sclerophyll-dominated slopes and flats near the Miocene basins of plant accumulation were bordered by a mixed conifer forest dominated by *Sequoiadendron*, with associates of *Abies* (*concolor*, *magnificashastensis*),⁴ *Picea* (*breweriana*, *polita*), *Pinus* (*ponderosa*), *Pseudotsuga* (*menziesii*), and *Chamaecyparis* (*lawsoniana*) among the common conifers. Their associates included fossil species of *Acer*, *Alnus*, *Amelanchier*, *Crataegus*, *Fraxinus*, *Holodiscus*, *Mahonia*, *Platanus*, *Prunus*, *Populus*, *Rosa*, *Salix*, *Sorbus*, and others, as listed above under COMPOSITION. In addition, each flora also has a few forest taxa that indicate summer rain, notably *Acer* (*grandidentatum*, *saccharinum*), *Betula* (*lenta*, *papyrifera*), *Diospyros* (*virginiana*), *Hydrangea* (*aspera*) and *Platanus* (cf. *occidentalis*). More numerous members of this alliance are in floras of similar age to the north in Oregon, or to the west in California. Their poorer representation in the Nevada floras is chiefly due to nearby terrain that produced local rainshadows over these basins.

The Miocene occurrence of *Abies scherrii* with dominant evergreen sclerophyllous vegetation, and with mixed conifer forest on bordering nearby slopes, parallels the occurrence of *A. bracteata* in the Santa Lucia Mountains today (Fig. 2). In this regard, it is noteworthy that *A. bracteata* inhabits steep terrain, living chiefly in sites where it is protected from fire by rocky bluffs and cliffs. In such sites it is well removed from areas where it might contribute to a fossil record. The question may thus be posed: Is the rarity of *A. scherrii* in the fossil record to be attributed to its preference for well drained, rocky sites scattered in the ecotone between mixed conifer forest and broadleaved sclerophyll vegetation?

There are important differences between the Miocene and the modern communities. These can be understood if we first reconstruct the physical setting of the Miocene community.

CLIMATE

Santa Lucia fir ranges through the canyon live oak-tan oak-madrone sclerophyll vegetation, reaching up into the mixed conifer forest in the Santa Lucia Mountains at levels from 4,000 to 5,000 feet. This is shown by its occurrence with *Pinus lambertiana*, *P. ponderosa*, and *P. coulteri* at or near Cone Peak, with *Calocedrus decurrens* and *Pinus lambertiana* at or near Junipero Serra Peak, and with *Calocedrus decurrens*, *Pinus ponderosa*, and *P. coulteri* at South Ventana Cone. With certain qualifications noted below, thermal conditions in the ecotone from conifer forest to broadleaved sclerophyll forest may be considered to approximate Miocene temperatures. Temperatures can be determined from records at stations in the Sierra Nevada where mixed conifer forest interfingers with

⁴ Species in parenthesis are living plants that seem most nearly related to the fossils.

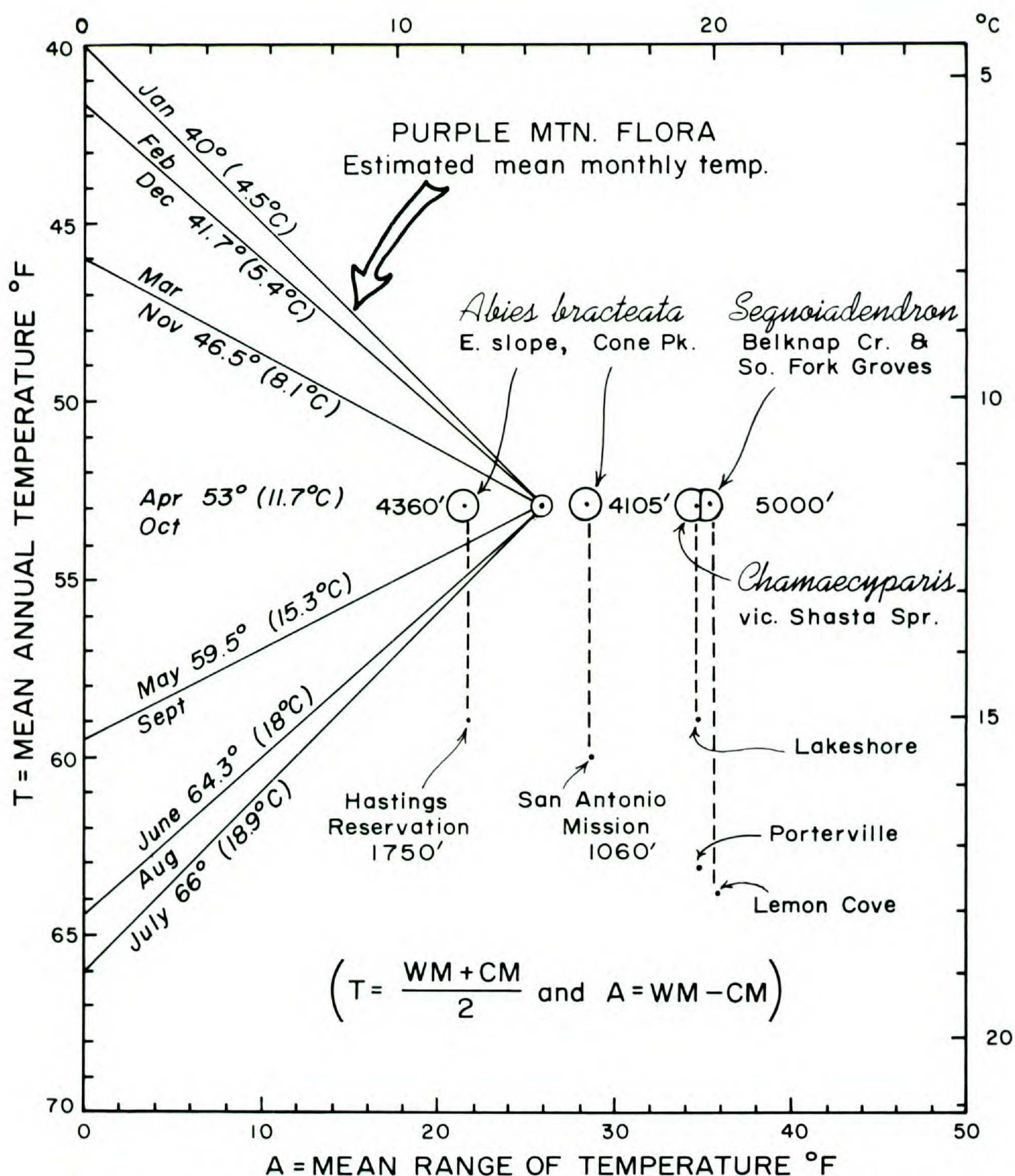


FIGURE 21. Estimate of thermal conditions under which fossil Santa Lucia fir lived during Late Miocene time. The data are based on present thermal conditions, modified by estimates of Miocene climate (see text).

broadleaved sclerophyll vegetation, and also by calculating temperatures for specific sites from stations in the adjacent lowlands to the west. Temperatures in the area of Santa Lucia fir can be estimated from meteorological records at stations in the nearby region to the east and north.

The latter method is illustrated in Figure 21. Temperatures for two stations with *Sequoiadendron*, Belknap Creek (4,800 ft.) and South Fork Grove (5,000 ft.) were calculated from temperatures at Lemon Cove (alt. 513 ft., $T = 63.9^\circ$, $A = 35.7^\circ\text{F}$) and Porterville (alt. 393 ft., $T = 63.2^\circ$, $A = 34.6^\circ\text{F}$), using a lapse rate

of 2.5°F per 1,000 feet.⁵ Figure 21 shows that they live under a mean temperature of $\sim 53^{\circ}\text{F}$. A similar result is suggested by data used to estimate conditions where Santa Lucia fir overlaps members of the Sierra mixed conifer forest at altitudes between 4,000 and 5,000 feet. There the stations selected are Hastings Reservation (alt. 1,750 feet, $T = 59.1^{\circ}$, $A = 21.5^{\circ}\text{F}$) and San Antonio Mission (alt. 1,060 ft., $T = 60.2^{\circ}$, $A = 28.4^{\circ}\text{F}$), utilizing a lapse rate of 2.5°F per 1,000 feet. The mean January and July temperatures estimated for the east slope of Cone Peak at 4,200 feet (see Fig. 21) are similar to those recorded there by Talley (1974) for those months in 1971. Significantly, this was a year in which temperatures at lowland stations in Salinas Valley to the east were close to the 30-year norm. Figure 21 also shows estimated temperature for the Shasta Springs area, where *Chamaecyparis* is in the ecotone between mixed conifer forest and broadleaved sclerophyll vegetation. The temperature was calculated from the records at Mt. Shasta City (alt. 3,544 ft., $T = 49.9^{\circ}$, $A = 34.7^{\circ}\text{F}$) and Lakeshore (alt. 1,075 ft., $T = 58.9^{\circ}$, $A = 34.8^{\circ}\text{F}$).

The range of temperature (A) in the Miocene was more nearly like that now in the forest-sclerophyll ecotone in the Coast Ranges than in the Sierra Nevada. This seems likely inasmuch as the fossil floras with *Abies scherrii* (cf. *bracteata*) all have a few taxa that live chiefly on the coastward slopes, notably *Picea* (cf. *breweriana*), *Chamaecyparis* (cf. *lawsoniana*), and *Castanopsis* (cf. *chrysophylla*) in northwestern California,⁶ or are found in the coastal strip farther south, as exemplified by *Cercocarpus* (cf. *blancheae*), *Lyonothamnus* and *Mahonia* (cf. *insularis*). Furthermore, with some summer rainfall over the region—as compared with clear, cloudless summer skies today—the cloud deck would reduce the high summer temperatures. Also, *Sequoia (sempervirens)* was then living on the coastward slope of the Sierra Nevada (Condit, 1944) 90 miles west of the Purple Mountain flora. Its occurrence there together with *Chamaecyparis*, *Lithocarpus*, *Persea*, and *Umbellularia* clearly implies a low range of temperature. By inference, comparable conditions must have extended inland since the northern Sierra was then only a low ridge without significant relief (Durrell, 1966: 192–195; Axelrod, 1956). Since the fossil floras with *Abies (bracteata)* represent an environment like that now in the ecotone between broadleaved sclerophyll and mixed conifer forest, thermal conditions there were approximately as shown in Fig. 21: mean annual temperature, 53°F ; mean range of temperature, 26°F ; mean July temperature, 66°F ; and mean January temperature 40°F . From these data it is estimated that the Miocene ecotone had an effective temperature (ET) or warmth (W) of 55.7°F , or 158 days with a mean temperature above 55.7°F .

⁵ Temperature normally decreases as altitude increases. In air free from the surface, the standard lapse rate is $-3.6^{\circ}\text{F}/1,000\text{ ft.}$ But close to the ground, heat is supplied to the overlying air during the day, so air temperatures measured in the instrument shelter record conditions warmer than those in free air. This “ground effect” thus reduced the lapse rate, and gives a “terrestrial” lapse rate that approximates $3.0^{\circ}\text{F}/1,000\text{ ft.}$ under normal conditions (H. P. Bailey, written communication, Jan., 1975).

⁶ The scrub form, var. *minor*, occurs to the south Coast Ranges. The tree form var. *chrysophylla* has a relict occurrence in the Sierra Nevada near Pino Grande, Placer County, in the lower part of the mixed conifer forest where it is associated with *Quercus chrysolepsis*, *Lithocarpus densiflorus*, and *Arbutus menziesii*.

The temperateness index was M 57, and about 4% of the hours of the year had frost (see Bailey, 1960, 1964).

It is emphasized that Miocene thermal conditions differed from present ones in two important ways. *First*, winters must have been more mild because ice caps were not yet in existence and hence cold and freezing conditions (like the winter ice storm of 1974) were not yet present. *Second*, in view of warmer Miocene seas, summers were moist and warm, high evaporation such as exists today could not have been present, and hence summer temperatures were more moderate than those of today. The temperatures estimated above must therefore be *extreme* for the Late Miocene. Clearly, temperatures were more equable than those now in the ecotone from mixed conifer forest to broadleaved sclerophyll vegetation at altitudes near 4,000–5,000 feet in the Santa Lucia Mountains where *Abies bracteata* lives today.

Precipitation in the mixed conifer–evergreen sclerophyll forest ecotone near 4,000 feet in the Santa Lucia Mountains is about 35–40 inches, distributed chiefly in the winter season as rain, and occasionally as light snow. As noted earlier, there was some summer rainfall over western Nevada during the Late Miocene, probably amounting to several inches for the summer season. The minimum rainfall required to support the flora can be estimated also from the temperatures suggested above for the Miocene ecotone. Using a mean temperature (T) of 53°F and a range of temperature (A) of 26°F , the Water Need (N), which is based on the exponential relation between temperature and moisture (see Bailey, 1958), calls for a minimum precipitation of about 35 inches, including that of the summer season.

ALTITUDE

The general altitude of the lake basins in western Nevada that were situated in the ecotone between mixed conifer forest and broadleaved sclerophyll vegetation was estimated earlier to be near 2,000 to 2,500 feet. This was based on the general relations of vegetation and climate, and on evidence that a major rain-shadow like that of the present had not yet developed (Axelrod, 1956).

Altitude can also be estimated by comparing thermal conditions in the Miocene of Nevada with that at sea level to the west, and interpolating altitude from the difference in mean temperature (Axelrod, 1965, 1968). As estimated above, thermal conditions in the forest-sclerophyll ecotone were approximately T 53°F and A 26°F . During the Late Miocene the coastal strip had a mean temperature near 60° to 61°F as judged from the slightly younger Neroly flora of western California that resembles vegetation in coastal Virginia (Condit, 1938). Temperatures were somewhat warmer during the Middle Miocene (~ 15 m.y.) as judged from the Temblor flora near Coalinga (Rennie, 1972) which is situated 145 miles southeast of the Neroly flora. It shows relationship to vegetation in coastal North Carolina, where mean temperature is 62° to 63°F . Assuming a Late Miocene terrestrial lapse rate of 3.0°F per 1,000 feet (or $1^{\circ} = 333$ feet), a difference in mean temperature of approximately 7°F – 8°F between the Purple Mountain flora and the Miocene floras at sea level implies a minimum altitude of about 2,300–2,600 feet. Realizing that this is an estimate, it seems likely that the Purple

Mountain flora had an altitude near 2,500 feet. This agrees closely with earlier estimates for the Fallon and Chloropagus floras of the nearby region, estimates based on very different lines of reasoning (Axelrod, 1956).

POST-MIOCENE CHANGES

The mixed conifer forest that inhabited cooler, moister slopes and valleys bordering the sclerophyll-dominated basins was richer than the modern descendant vegetation. It included conifers related to those that are now restricted in area, notably *Picea breweriana* and *Chamaecyparis lawsoniana* that are confined to northwestern California, *Sequoiadendron giganteum* which lives in the central and southern Sierra Nevada, as well as *Abies magnifica* and *Pinus monticola* that now occur in subalpine sites in the Sierra Nevada well removed from Santa Lucia fir today. Similar relations are displayed by the broadleaved sclerophyll vegetation, for the Miocene community included species similar to those now in coastal southern California, notably species of *Cercocarpus*, *Lyonothamnus*, and *Mahonia*. Furthermore, both vegetation zones had a few species related to those now in areas with summer rain.

The emergence of modern communities of lower diversity and more restricted area is due to the gradual development of new moisture-thermal conditions during the Pliocene which culminated in the appearance of summer-dry mediterranean climate in the middle and late Quaternary. Increasing summer drought has resulted in progressively greater water stress during the critical period of seedling germination, growth, and establishment (Axelrod, 1976). Hence, taxa that were unable to adapt to these new conditions in the lower part of the mixed conifer forest near broadleaved evergreen sclerophyll vegetation were gradually confined to areas in which they could reproduce successfully. The regular occurrence in the Miocene of such "subalpine" species as *Abies* (*magnifica*), *Pinus* (*monticola*), *Tsuga* (*mertensiana*) and *Populus* (*tremuloides*) with mixed conifer forest taxa as *Abies* (*concolor*), *Pinus* (*ponderosa*), *Calocedrus* (*decurrens*), and *Sequoiadendron* (*giganteum*), and with broadleaved sclerophylls as *Quercus* (*chrysolepis*, *wislizenii*), *Castanopsis* (*chrysophylla*), *Lithocarpus* (*densiflorus*), *Arbutus* (*menziesii*), in the same fossil flora, is symptomatic of the nature of the post-Miocene changes in community composition that were due to changing climate, and chiefly to increased water deficit in the summer season. Its effect can be summarized in terms of the modifications that appear to account for the distributions of taxa whose Miocene relatives were associated with fossil Santa Lucia fir, and which now define the segregate communities of lower diversity that are confined to more local areas.

Sierra redwood (*Sequoiadendron*), which is restricted to the central and southern Sierra Nevada, probably entered the range following the Late Miocene as rainfall decreased and as conditions became sunnier there. *Sequoiadendron* is now known from the Middle Pliocene Mount Reba flora (7 m.y.), Alpine County. The site is at wind timberline, above a subalpine forest of *Abies magnifica*, *Pinus monticola*, and *Tsuga mertensiana*. The Mt. Reba flora is dominated by broadleaved sclerophyllous evergreens, as shown by the abundance of specimens of *Quercus* (*chrysolepis*), *Lithocarpus* (*densiflora*), and *Cupressus* (*cashmeriana*).

Pseudotsuga (menziesii) is also common, and probably formed rich stands on nearby slopes much as it does today at levels near 2,000–2,500 feet in the lower foothills of the range. A few scraps of other conifers are present, notably *Abies (concolor)* and *Sequoiadendron*. The community shifted to lower levels as colder climates developed as the range was elevated later in the Pliocene and during the Quaternary.

Reasons for the present absence of *Sequoiadendron* in the Sierra Nevada north of the American River drainage (Placer County) are not clear. However, the region receives much higher rainfall, and a number of taxa that are typical of forests in the Coast Ranges occur in the northern Sierra Nevada. This gives to the mixed conifer forest of that area a denser, richer understory of shrubs and small trees than in the Sierra farther south. As a result, relatively less light falls on the forest floor, and conditions are therefore unfavorable for taxa that are light demanding, especially in the seedling stage. That Sierra redwood seedlings thrive best under conditions of ample light is apparent from the heavy reproduction that occurs about the margin of moist meadows in the southern Sierra today, as at Balch Park in Tulare County, east of Exeter. This agrees with the experimental studies by Stark (1968a) who noted “growth in full sunlight was superior to that in any shady forest” (p. 91) and that “healthy . . . seedlings grow best in full sunlight” p. 92). Stark (1968b: 276) also noted that the failure of trees to spread and expand their present range is the result of fire-suppression over the past decades, with the accumulation of a deeper-than-normal litter, as well as an increase in growth of understory shrubs and trees, and hence an increase also of shade within the forest.

One other point is to be noted in terms of the need of *Sequoiadendron* seedlings for ample light. Sierra redwood occurs at numerous sites in the Miocene of Nevada and also at a locality (Trapper Creek) in southeastern Idaho. However, it has not been recorded in any of the Miocene floras that are scattered widely in Oregon, Washington, and western Idaho. The floras of that region are richer in taxa than in the area to the south chiefly because of the higher precipitation there. Mesic conifers (*Cephalotaxus*, *Ginkgo*, *Glyptostrobus*, *Metasequoia*, *Sequoia*, *Taxodium*) are present in most of these floras, and deciduous hardwoods are especially abundant together with some associated broadleaved evergreens. But in the Miocene floras to the south, mesic conifers are rare to absent, deciduous hardwoods have a poorer representation, and sclerophyllous taxa increase in diversity and abundance. These relations imply climate was drier and sunnier to the south, which is consistent with the composition of the Miocene floras in the Mohave region where live oak woodland and thorn scrub are wholly dominant (Axelrod, 1958). The general distribution of *Sequoiadendron* during the Miocene is therefore consistent with conditions that it seems to require for best reproduction—ample light and sufficient moisture during the critical stage of seedling establishment.

Taxa that are often considered “subalpine indicators,” notably *Abies magnifica*, *Picea breweriana*, *Pinus monticola*, *Tsuga mertensiana*, *Populus tremuloides*, and others, have close relatives in the Miocene floras of Nevada where they occur with sclerophyllous taxa and fossil Santa Lucia fir. Since geologic evidence shows

that these plants lived in terrains of low relief, and since "subalpine" species are sufficiently abundant numerically to form codominants of some of the fossil floras, they must have lived near at hand (Axelrod, 1976). This means they were regular members of the mixed conifer forest. Such an occurrence is consistent with the presence of most of their living descendants in mixed conifer forest in areas to the north, where there is more rainfall in summer, a longer precipitation season, and a lower evaporation rate (Axelrod, 1976). The taxa that are now confined to subalpine forest in the Sierra evidently were restricted to that zone as dry summer, montane mediterranean-type climate spread during the later interglacial ages. Thus, the distinctness of the modern subalpine (or pure conifer) forest in the Sierra Nevada is due to the restriction of its taxa to this higher, cooler zone where the effect of high evaporation (= water deficit = water stress) is less than in the mixed conifer forest at lower levels, a forest from which they are now largely excluded.

The confinement of *Abies bracteata* to the Santa Lucia Mountains seems consistent with its mild climate and lower evaporation rate in summer as compared with the Sierra where many of its former associates occur. In this regard, the forested parts of the outer Coast Ranges have lower summer temperature and milder winters than comparable parts of the Sierra (Fig. 21). Thus, Santa Lucia fir may have been eliminated from the Sierra Nevada, where it probably occurred during the Pliocene, by the high evaporation rate in summer which was inimical to seedling establishment. A second factor was increasing winter cold with accompanying snow and ice. That it would have had a disastrous effect on the trees at higher levels in the ecotone between mixed evergreen forest and mixed conifer forest may be inferred from the severe damage inflicted by the snow and ice storm on Santa Lucia fir during the winter of 1974, which resulted in numerous broken tops (with cones) and limbs (oral communication, S. Talley, 1974). Similar damage was inflicted on its broadleaved evergreen associates, notably *Arbutus menziesii*, *Lithocarpus densiflorus*, *Quercus chrysolepis*, and *Q. wislizenii*. On this basis we may infer that conditions probably were too severe for *A. bracteata* in the Sierra Nevada during the glacial ages. In this regard, its present absence from the Coast Ranges farther north may reflect the more severe winters there, for the frequency of snow increases northward and the mean January temperature rapidly falls below 40°F, which appears to be near the minimum for the species today (Fig. 21).

The present absence of Santa Lucia fir farther south in the Coast Ranges may reflect a recent restriction in range. It may possibly have been eliminated there by the xerothermic periods of the later Quaternary (Axelrod, 1966: 42–55). This seems consistent with the paucity of conifer forest taxa in the isolated areas where forest now occurs in the central Coast Ranges (Axelrod, 1976). Altitudes in these areas, whether in the Santa Cruz or Santa Lucia mountains or the interior Diablo and La Panza ranges, are relatively low and the forest has only one or two species. However, in the higher north Coast Ranges (north of Clear Lake), the Sierra Nevada, the Transverse Ranges and Peninsular Ranges of southern California, the forest has mixed stands of several conifers. It seems

likely that a warm dry xerothermic period would have eliminated many forest taxa from the central Coast Ranges simply because terrain was not sufficiently high to provide cool, moist sites for them, and hence they disappeared because drought stress militated against successful reproduction.

That richer, more diverse forests were in the region earlier is shown by the occurrence of *Calocedrus decurrens* and *Pinus lambertiana* in the Santa Cruz Mountains during the Plio-Pleistocene transition (Dorf, 1930: 18). This may also be inferred from the occurrence of a rich mixed conifer forest on the valley floor near San Jacinto in southern California (Axelrod, 1966), a region now semi-desert. The occurrence of *Sequoia sempervirens* and *Pseudotsuga menziesii* along the Santa Barbara coast during the late Quaternary (Axelrod, 1967: 295–296), and the present relict stand of mixed evergreen forest (*Arbutus menziesii*, *Quercus chrysolepsis*, *Lithocarpus densiflorus*) in the nearby summit section of the Santa Ynez Range at San Marcos Pass also provide hints of the nature of the forests that probably inhabited the central Coast Ranges during the cooler, moister phases of the Quaternary.

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